Impacts of Disturbances on Species Specific Interactions between Crabs and Plants in Mangrove Ecosystems

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Chapter 6

Synthesis and Conclusion

This thesis aimed to provide an increased understanding on the functioning of mangrove ecosystems, and particularly of mangrove crab-vegetation interactions, upon disturbance. To this aim, we performed a novel combination of a field survey, field manipulation experiments as well as lab and mesocosms experiments to comprehensively determine crab-vegetation interactions as well as their impacts on mangrove ecosystem functioning. The field survey (Chapter 2) showed that severely disturbed mangrove system contained a significantly lower mangrove tree cover, higher understory cover, more open/unvegetated areas and lower crab abundances compared to the undisturbed systems. At the same time though, no significant differences in total vegetation cover, in plant species richness or in crab species richness had occurred. Multivariate analysis of our field data also provided the first hints about the importance of species-specific crab-vegetation interactions, as some of the sympatric crab species of the same genus had opposite preferences for certain mangrove plant species, occurring at either disturbed or to undisturbed ecosystems. Our feeding experiments (Chapter 3) provided a deeper understanding of the drivers leading to these species-specific preferences: We found that plant species identity is a major driver of the variation in the consumption of mangrove leaf litter and green mangrove leaves, while propagule predation was driven by mangrove plant-crab species specific interactions. The results of the feeding experiments in the laboratory coincided with the results of our field survey and provide an explanation for why certain crab species seem to relate to particular plant species or why certain plant species attract particular mangrove crab species. Further field experimentation in different disturbance mediated gaps (Chapter 4) revealed the importance of mangrove plant-crab species-specific interactions in propagule predation, despite a significant role of crab presence itself on propagule availability. Due to this species-specific propagule predation, the dominant vegetation of the disturbed areas was favored, which may strongly hamper the natural restoration of the severely disturbed mangrove ecosystems. And finally, the design of our mesocosms experiment (Chapter 5) enabled differentiating between the significant impacts of crab presence on, on the one hand increasing mangrove litter decomposition from, on the other hand, the impacts of grazing of mangrove green leaves (causing a loss of vegetation biomass). Prevailing theory suggests that increased litter decomposition would increase nutrient availability to sustain vegetation growth, but we found no significant impact of crab presence on mangrove productivity. Below, I will discuss the most important implications of this thesis as gained by combining results from different individual chapters and will finish with the key conclusions of this work.

1. Importance of species-specific interactions for the functioning of mangrove ecosystems

Despite the many claims on the importance of mangrove crabs in the structuring and the functioning of mangrove ecosystems (Andreetta et al. 2014), our results show that mangrove plants are the major driver in determining the productivity of the system (Chapter 5) as well as determining the decomposition rates of their litter (Chapter 3). Given the key role of these processes in the functioning of mangrove ecosystems in general, it seems likely that the species identity of mangrove vegetation plays a critical role in determining many carbon and nutrient related ecosystem processes (Gleason and Ewel 2002, Bouillon et al. 2008). This implies that significant changes in the species composition of mangrove vegetation could potentially alter various ecosystem processes. For instance, the productivity and relative growth rates were higher for species from the undisturbed mangrove ecosystems compared to those plant species from disturbed sites (Chapter 5). Whether these differences will have positive or negative impacts on the ecosystem's biomass will also depend on the vegetation composition as was evident for the significantly higher total crab consumption rates of leaves of the dominant plant species of undisturbed areas (Chapter 3).

At the same time though, the presence of mangrove crabs within the system significantly increased the leaf litter decomposition rates of the non-recalcitrant mangroves (Chapter 5). Our long term (90 days) mesocosms experiments confirmed the results of the short term (48 hours) laboratory feeding experiments which revealed crab's preferences for the green leaves of the poorly decomposable *Rhizophora apiculata* and *Derris trifoliata*. In addition, they significantly consumed more leaf litter of the non-recalcitrant plant species. On the other hand, mangrove crab species that dominantly occurred in the disturbed areas (Chapter 2) consumed more green leaves (Chapter 3) compared to crabs that were dominantly present in the undisturbed areas. This was again reflected in their grazing on green leaves of *Derris trifoliata* in the mesocosms experiments (Chapter 5). This consistent pattern indicates consistent species-specific mangrove crab-plant species interactions with regards to crab feeding strategies on mangrove leaves despite the superiority of plant species identity as the major driver of the productivity and decomposition in mangrove ecosystems.

On the other hand, our results also show how species-specific crab-plant interactions drive propagule predation. The identity of the crab-plant species interactions involved was identified as the major driver. This means that the decrease or increase in one of the interacting components could either decrease or increase propagule predation, depending on the identity of the other component. In this study, the propagule predation by mangrove crabs negatively affected the dominant plant species of the undisturbed ecosystems, *Rhizophora apiculata* and *Bruguiera parviflora*. In contrast, the dominant species of the disturbed system, *Derris trifoliata*, was less consumed by the mangrove crab community (Chapter 3). This result was confirmed in the disturbance mediated gaps experiment (Chapter 4) where the propagules of *Derris trifoliata* were significantly less consumed compared to the propagules of *Rhizophora apiculata* and *Bruguiera parviflora*. In the disturbed mangrove ecosystems, seedling availability of *Rhizophora apiculata* and *Bruguiera parviflora* was lower than presumably demanded for natural recovery due to a combination of higher predation and initially lower seed availability. These results seem to explain the prevalence of *Derris trifoliata* dominating the disturbed mangrove areas and seem to contribute to the inability of the system to recover naturally after severe disturbances.

The dominance of plant species identity as major driver of mangrove crab feeding and therefore of nutrient recycling, suggests that they play an important role as ecosystem engineer. Indeed, the removal of mangrove trees through cutting altered the disturbed system such that it became significantly different from the undisturbed system (Chapter 2). Tree cutting replaced mangrove trees and promoted dominance of understory shrubs with a different substrate quality for herbivores and decomposers. As substrate quality of mangrove plant species was the major driver in the leaf litter consumption by the mangrove crab community, the change in the mangrove plant diversity within a system could be the ultimate cause of the significant impact found on the mangrove crab community: total mangrove crab abundances decreased in the disturbed mangrove areas compared to the undisturbed areas while no significant decrease in both mangrove plant and mangrove crab species richness had been found. Also the species composition of the crab community changed as two sympatric crab species responding differently to disturbances, as shown in the RDA analysis of Chapter 2. *Perisesarma semperi* and *Episesarma singaporense* preferred the disturbed system dominated by the shrub understory species *Derris trifoliata* while their sympatric species *Perisesarma indiarum* and *Episesarma versicolor* preferred the undisturbed areas dominated by mangrove trees species.

2. Nutrient recycling and productivity of mangrove ecosystems as affected by species-specific interactions

Our mesocosm study extends and deepens our understanding on the nature of mangrove plant-crab interactions and their impacts on nutrient recycling and the productivity of mangrove ecosystems. Mangrove crabs feeding on different mangrove substrates play a double role in affecting mangrove primary production. The presence of mangrove crabs in our mesocosms did not only significantly increase mangrove leaf litter decomposition rates but also increased mangrove biomass loss through their grazing on mangrove green leaves. However, these impacts were not reflected in nutrient mineralization or on the overall mangrove growth rates. Instead, mangrove plant species identity had a more significant impact on their relative growth rates (Chapter 5). Our results also indicate the dominant role of mangrove plant species –instead of the supposed mangrove crabs- in overall nutrient recycling and productivity of the mangrove ecosystem. Nevertheless, the mangrove crab community did also play an important role in processing mangrove primary production through feeding on the leaf litter and through grazing of mangrove green leaves. However, mangrove plant species identity was a major driver of mangrove crab feeding and therefore the nutrient recycling following this process, but also in their productivity.

Previous field studies emphasized the importance of litter removal and consumption by the mangrove crab community (Robertson and Daniel 1989, Micheli 1993) and another study examined the roles of certain crab species in green leaf herbivory (Farnsworth and Aaron 1991). Through our mesocosm set-up, we were able to simultaneously analyze and differentiate among these two roles. Surprisingly, and in contrast to claims in literature, crabs deliberately grazed on the green leaves of the recalcitrant mangrove species *Rhizophora apiculata* and *Derris trifoliata* rather than feeding on the presumably more palatable leaf litter provided at the beginning of the treatment. In this study, mangrove crabs consistently consumed more green leaves of *Derris trifoliata* both in the laboratory experiment of 48 hours (Chapter 3) and in the mesocosms experiment (Chapter 5) lasting for 3 months. Similarly, mangrove crabs grazed more on the green leaves of *Rhizophora apiculata* than they fed on the decomposed leaf litter provided in the mesocosms. The extent to which this occurred was, however, crab-species dependent. This finding indicates that grazing on the green leaves could be the important strategy in relation to the nutrient recycling for the recalcitrant plant materials.

We found a significant positive impact of mangrove crabs on litter decomposition rates. However we were unable to detect significant impacts of mangrove crab presence on the relative growth rates of different mangrove plant species. The relative contribution of nutrients supplied by decomposition of mangrove leaf litter or mangrove crab feeding on green leaves were very small compared to the total amount of nutrients supplied by the mineralization of soil organic matter provided in the mesocosms, and thus did not generate significant impacts. However the significant differences in the decomposition rates in the presence of crabs compared to those in the absence of crabs suggests that mangrove crabs could in the long term play an important role in the recycling of nutrients that are occluded in the biomass of mangrove species primary production, but not at the short term.

3. The success of mangrove ecosystem restoration after disturbance also depends on these species-specific interactions

Our gap experiments in the field showed that propagule predation by mangrove crabs was the dominant factor limiting the ability of disturbed mangrove ecosystems to recover naturally: Mangrove crabs were able to consume more than 90% of the mangrove propagules being planted in the disturbance mediated gaps during the first four weeks after planting. This result is in line with and confirms our feeding experiment which showed that crab predation on mangrove propagules was higher compared to crabs feeding on mangrove leaves (Chapter 3). Our feeding experiment already showed that crab feeding on propagules was also species specific. The nature of species-specific interactions between crabs and mangrove propagules has a more significant impact on propagule predation compared to crab or mangrove species identities alone. This species-specific interaction suggests that certain crabs prefer particular propagules, disregarding the common rule concerning the dominance of chemical or physical properties of propagules in determining their susceptibility to predation. In contrast to what might be expected, the higher N content of *Derris trifoliata* compared to other propagules in this study did not promote crab predation. In addition, the higher tannin content and bigger physical size of *Rhizopora apiculata* propagules did not prevent high consumption by crabs, even by *Perisesarma indiarum* which has a small body size. These findings demonstrate that common rules concerning the role of chemical and physical properties in determining predation rates do not apply to mangrove propagules.

However, we found that crab feeding on mangrove propagules had relatively little effect on the dominant mangrove understory species of the disturbed areas (*Derris trifoliate)* while it had strong negative effects on the propagules of dominant mangrove species of the undisturbed areas. Our gap experiment thus confirmed what was found in the laboratory (Chapter 3). Propagule predation was high for almost each mangrove species except for the dominant mangrove species of the disturbed areas, *Derris trifoliata*. Mangrove disturbance in the form of mangrove tree cutting decreased propagule availability. High predation on mangrove propagules decreased the potential of mangrove recovery after disturbance and favored the understory species *Derris trifoliata* to prevail over the disturbance mediated gaps. Moreover, mangrove crabs do not prefer propagules of *Derris trifoliata* which therefore increases the chance of this understory mangrove to dominate the disturbed areas. At undisturbed conditions, however, the presence *Derris trifoliata* was fully controlled by the mangrove trees canopy, taking away the necessary resources for *Derris trifoliata* to prosper. However, when the system was severely disturbed through mangrove trees cutting, this understory species quickly flourished through their vegetative growth amplified by the lower propagule attacks by mangrove crabs.

4. Towards a generic understanding and application of species-specific interactions in mangrove ecosystem restoration

Many mangrove ecosystems are heavily disturbed and endangered to the point of no return to their original undisturbed state. Our study indicates that the inability of the severely disturbed mangrove ecosystem to recover seems to be the result of several interconnected factors related to mangrove plant-crab interactions: Under undisturbed conditions, mangrove plant-crab interactions seem to promote nutrient recycling through higher decomposition rates of mangrove leaf litter and the grazing of green mangrove leaves. On the other hand, the increasing mangrove understory cover under the disturbed condition inversely correlated to mangrove crab abundance in the field suggesting lower leaf litter consumption rates and therefore lower nutrient recycling and lower mangrove primary productivity. However, we were unable to demonstrate a significant impact of the mangrove crab community on the productivity of mangrove ecosystems, despite a significant impact of mangrove plant species identity. On the other hand, mangrove crab-plant species specific interactions drive propagule predation and favors mangrove understory species that are dominantly present after severe disturbances. This finding indicates that mangrove plant-crab species specific interactions could prevent the natural recovery of the disturbed system and even cause the disturbed system to go further away from its original undisturbed state. All together our results indicate the importance of maintaining mangrove plant diversity as the first step to preserve mangrove ecosystem functioning.

As mangrove forests in Indonesia and in other parts of the world are increasingly disturbed, further studies need to be done to test whether our findings can be applied to other disturbed mangrove systems in other places such in other islands of Indonesia, or other parts of the world.

Expanding these studies to other mangrove ecosystems, especially to mangrove systems with greater species richness and different extents of disturbances, will enable us to simultaneously evaluate the importance of plant-crab species-specific interactions. It is expected that the number of species-specific interactions will increase from a monoculture mangrove system via the species poor conditions of severely disturbed mangrove systems such in Segara Anakan to more pristine conditions. These studies may provide answers to the following questions: Is lower crab density related to disturbed mangrove systems or to the lower plant diversity per se such as occurring in monoculture mangrove systems? Will mangrove plant species richness, through an increased number of species-specific interactions, positively relate to crab species richness? In addition, it will allow determining some of the impacts related to increased species richness and increased species interactions. For instance, a small/scale previous study (being part of Chapter 4) indicated that a monoculture stand considerably reduced the recruitment of propagules of other species. Is the recruitment of the dominant mangrove species always favored or do other factors determine the process? What is the relative role of increased species richness vs. species interactions on the various ecosystem processes?

Related to the above mentioned issues is the question whether it is possible to apply crab diversity of abundance as a bio-ecological indicator. So far, a limited study was unable to reveal the applicability of crabs as bio-ecological indicator (Geist et al. 2012). Our results do, however, point into that direction. So, the question seems to be at what scale (meter squares, hectares, km squares) will crab abundance become a bio-ecological indicator? Comparing mangrove crab species richness, abundances and its functional diversity at different scales of disturbance and at different places or islands will likely reveal the feasibility of crabs as bio-ecological indicator.

Currently, there is no long term study that has examined soil quality related to nutrient recycling in disturbed mangrove systems compared to the undisturbed one. Again, our study suggests that differences may occur, due to both the differences in species identity as well as in species interactions. An open question is, however, whether the undisturbed mangrove system will sequester more carbon in its sediment compared to a disturbed system? Also with regards to this aspect, only one study has been performed, which showed that a mixed culture mangrove stand sequestered more sediment carbon compared to a monoculture stand despite a lower carbon accumulation in standing biomass (Chen et al. 2012). Our mesocosm study showed that crabs play a significant role in mangrove litter decomposition and herbivory. However, we were unable to detect a significant impact on the retention of mangrove soil nutrients. Whether the mangrove crab community really plays a significant role in carbon sequestration and soil nutrient retention and whether it positively correlates to greater mangrove species richness remains a critical question to answer.

5. Conclusions

This thesis evaluated the impacts of shifts in vegetation composition in mangrove ecosystems, due to disturbance, on the interactions between crabs and plants. These two major and important components within mangrove ecosystems are known to be mutually connected to each other. We showed that, next to their role in litter decomposition, crabs also critically affect green leaf biomass of particular plant species in mangrove ecosystems and that they severely predate on mangrove propagules. Moreover, we showed that despite their impact on litter decomposition (and presumed enhanced nutrient availability), there was hardly any impact of crab feeding on vegetation productivity. Instead, the results of our mesocosm experiment showed that plant species identity plays a dominant role in determining their growth rates. In contrast, crab feeding plays a critical role in propagule predation, hitherto not appreciated. Propagule predation was shown to be driven by highly species-specific plant-crab interactions (as was the consumption of green leaves and leaf litter).

Mangrove disturbances significantly altered vegetation composition and decreased crab abundances in the disturbed areas compared to the undisturbed areas. As a consequence, the nature and consequences of crab-plant interactions also changed. Our analysis revealed that while mangrove crab-plant interactions are important in undisturbed mangrove ecosystem, they are even more crucial in disturbed mangrove ecosystems. Crab feeding on mangrove leaf litter is significantly higher on the dominant plant species of the undisturbed area compared to those of the disturbed areas, while they fed more heavily on green leaves of the dominant plant species of the disturbed areas. Moreover, propagule predation by crabs favors the dominant plant species of the disturbed areas and disfavor those dominantly present in the undisturbed areas. Altered plant-crab interactions may therefore in the long run benefit understory species like *Derris trifoliata* to remain dominant and push the disturbed mangrove ecosystem further away from its original undisturbed state. These findings may have serious consequences for the restoration of heavily disturbed mangrove ecosystems.

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